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Regeneration in Phegopteris polypodioides*

ELIZABETH WUIST BROWN

(WITH THREE TEXT FIGURES)

INTRODUCTION

The fact that plants are able to reproduce lost parts was known long before it was discovered that animals possessed this same power. It was natural that the first experimental investigation on regeneration in plants should have been carried on with the higher plants as it was a common practise to propagate many plants by means of cuttings. However, the study of regeneration has since been extended to include not only the lower groups of plants, such as the algae, fungi, liverworts, mosses and ferns, but also many groups of animals. This has resulted in the accumulation of a large amount of evidence regarding the possibilities of regeneration by most groups of organisms.

Experimental evidence has also indicated that the regenerative power of some plants is much greater in earlier than later life, while in others this power is lost completely in later life.

Goebel (2, pp. 196–203), experimenting with ferns, found that the primary leaves of the young sporophytes of some ferns, either while attached to the sporophyte or cut off and placed under moist conditions, were able to regenerate new fern plants or prothallia or intermediate forms between leaves and prothallia. Here the regenerative power seemed confined to the primary

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* Contribution from the Osborn Botanical Laboratory.

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leaves of the young sporophytes, as in no case did regeneration take place with leaves of the older plants. It was thought of interest to see if the primary leaves of the young sporophytes of *Phegopteris polypodioides* Fée could regenerate in the manner indicated by Goebel, as apogamy had occurred so frequently in cultures of this fern.

EXPERIMENTAL

Spores of *Phegopteris polypodioides* were obtained from Brooklin, Maine, through the kindness of Dr. A. H. Graves. Cultures were started in the early part of October. The spores were sown on Prantl's and Knop's full nutrient solutions and modifications of these solutions. After the spores were sown the cultures were placed before an east window. In an effort to induce apogamy the prothallia were not transferred to fresh nutrient solutions from time to time, but were allowed to develop upon the same nutrient solutions upon which the spores had been sown. As a result growth and development of the prothallia was slower and fewer sporophytes formed, the majority of which were apogamous.* The primary leaves of both normal and apogamous young sporophytes were used in the regeneration experiments.

March 14, 1917, primary leaves 5–7 mm. in length were cut from the young sporophytes and placed on sand in watch glasses. In some cases the petiole of the leaf was inserted in the sand to a depth of 1–2 mm., placing the blade of the leaf in an upright position. In other cases the leaf was laid on the sand; while in still others various parts of the blades were covered with the sand. The sand in some of the watch glasses was moistened with Knop's and Prantl's full nutrient solutions, while in the others it was moistened with distilled water. All the cultures were placed in large plates and covered with bell jars. The sand was never allowed to dry and water was kept standing in the plates. In this way the air under the bell jar was always moist.

No experiments were tried to see if the leaves would regenerate while attached to the young sporophytes and no such cases were observed among either the solution or soil cultures, although frequently the leaves of this and other species of ferns, especially in

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*Wuist, Elizabeth Dorothy. Apogamy in *Phegopteris polypodioides* Fée, *Osmunda cinnamomea* L., and *O. Claytoniana* L. Bot. Gaz. 64: 435. 1917.

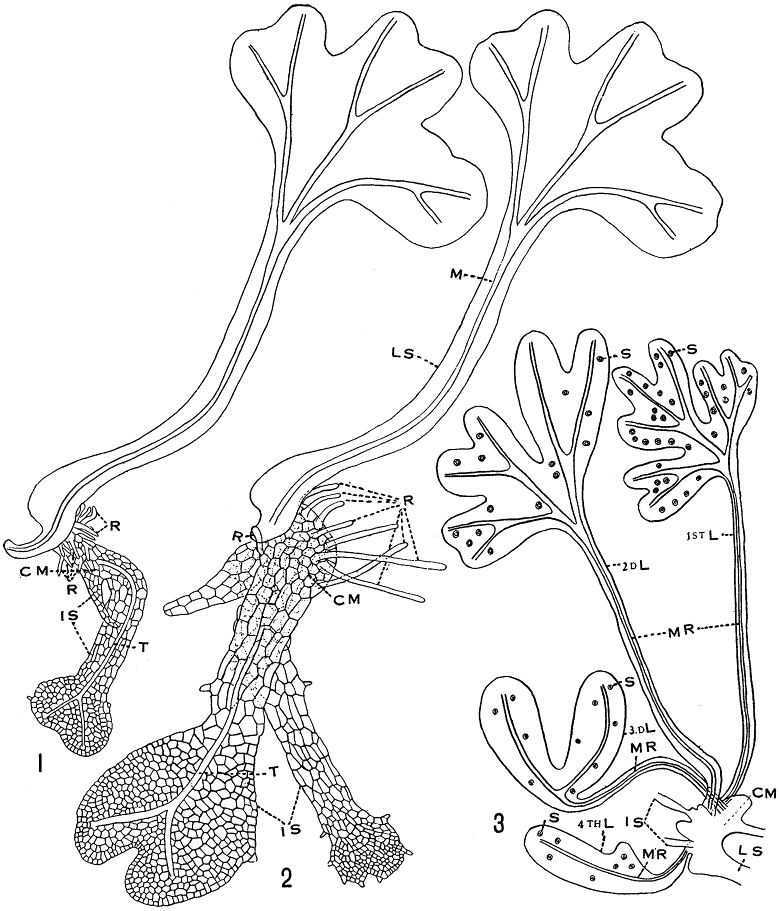
the soil cultures became appressed to the soil as a result of accidents in watering.

Only one case of regeneration was obtained, although a large number of leaves were experimented with. Regeneration began in about six weeks after the leaf had been removed from the sporophyte and laid on sand moistened with Knop's full nutrient solution. One side of the petiole, near its base, was destroyed by decay, and a short distance above this point on the opposite side of the petiole a slight swelling occurred, from which a cellular mass developed. At first it was slightly elongated, FIG. 1, afterwards it became much thickened and broadened, FIG. 2, and finally assumed the shape shown in FIG. 3. From this cellular mass there developed two intermediate structures between leaves and prothallia, then rhizoids and four normal leaves. Neither a true root nor a stem "Anlage" was formed.

The first of the intermediate structures resembled a very much elongated prothallium, one cell in thickness, with an expanded heart-shaped apex. Tracheids arranged in rows resembling a true midrib extended up through the portion of the structure corresponding to the petiole into the expanded or blade-like part. Here the rows of tracheids branched dichotomously one branch going to each lobe (FIGS. 1 and 2). The margins of both the elongated and expanded regions were for the most part smooth, with the exception of two papillae, one of which developed on the elongated and one on the expanded part.

The second intermediate structure which developed from the cellular mass was even more thalloid in form and structure than the first one. Both the elongated and broadened portions like those of the first were only one cell in thickness. The expanded portion differed somewhat in appearance as it was not so distinctly heart-shaped and its margin bore many more papillae. There were no indications of tracheids present in either of the portions representing petiole or blade.

Growth was rapid and apparently normal in both of these intermediate structures, but the second one never attained the size of the first. Neither was long-lived, death occurring soon after the normal leaves began to develop. The rhizoids resembled in every way those of a normal fern gametophyte. They formed from the cells of both the upper and lower surfaces of the cellular mass, although the majority came from the upper surface cells. Their development began at about the same time as that of the intermediate structures.



FIGS. 1–3. Stages in the regeneration of the young leaf of a sporophyte of *Phegopteris polypodioides* Fée, x 550. *R*, rhizoids; *LS*, leaf of sporophyte; *CM*, cellular mass; *IS*, intermediate structure; *MR*, midrib; *T*, tracheids; *S*, stomata; *1st L*, first leaf; *2d L*, second leaf; *3d L*, third leaf; *4th L*, fourth leaf.

After a number of rhizoids had been formed from the surface cells of the mass, normal leaves began to develop. The first and second of the four leaves appeared almost simultaneously and their growth was very rapid. They resembled, in all respects, the leaves of a normal young sporophyte of this species of fern (FIG. 3); although the blade of the second leaf was somewhat simpler in form, having only two main divisions, each of which was lobed, instead of three main lobed divisions. However, such irregularities are to be noted in leaves of normal young sporophytes of this and other species of ferns. These two leaves attained a height of 6 mm. The third leaf, which was much slower in growth and development reached a height of only 4 mm. and was much simpler in form. The blade consisted of only two lobes, which were entire. The fourth leaf showed still greater simplicity in form and reached a height of only 3 mm. The blade was almost entire, with a slight lobe on the one side. The blades of these latter leaves, like those of the first and second ones, bore stomata.

DISCUSSION AND CONCLUSION

The various theories which account for regeneration, as advanced by the many writers on the subject, consider the following influences: (1) external influences to which the plant is subjected; (2) tendencies inherent in the plant body.

The factors considered as the possible controlling or influencing ones may be placed in the following classes: (1) nutrition disturbances; (2) wound stimuli; (3) changes in the water content; (4) the accumulation, at certain places, of definite formation substances; (5) the presence of dormant or latent rudiments; (6) correlation; (7) age and maturity of the parts; (8) form disturbance; (9) growth tension; (10) interruption of the functions of respiration, transpiration or photosynthesis; (11) isolation from the influence of the whole; (12) presence of enzymes which are responsible for the formation of the part regenerated.

The fact that regeneration was never observed in attached leaves of *Phegopteris polypodioides* and did occur in a leaf which had been separated from the plant would seem to indicate that the separation from the repressing influence of the plant body played an important part, as believed by Loeb (4, p. 153); although the fact that cases have occurred in other species of ferns when the leaves were still attached would not seem to refute this theory. Experimental evidence has shown that many species of ferns, either in the younger or older stages of their gametophytic or sporophytic life history and especially in the younger stages, does not always react in the same way to the same environmental conditions; but each has a sort of individualism which enables it to react in the way best fitted for its particular needs. It seems very probable that in this particular case regeneration is closely connected with nutrition for the reason that the severed leaf was not able to regenerate immediately another sporophyte, but could produce a cellular mass which appeared to be a reversion to a prothallus-like structure. This structure after rhizoids developed gave rise, in an apogamous manner, first to structures intermediate between leaves and prothallia; then, as the number of rhizoids increased, enlarging the absorptive surface, which in turn increased the amount of nourishment, true leaves were produced. The first of these were the ordinary type of young sporophytic leaf but later ones were much more primitive in character, due doubtless to the lowered vitality of the prothallus-like structure. This coincides with Goebel's (1, vol. 2, p. 42) views. He considers a reversion to a juvenile form as being the result of unfavorable conditions to which the plant is subjected. It is also in keeping with the results obtained by Miss Kupfer (3, p. 229) in her experiments, which indicated that at the time of cutting under normal conditions reserve food was present in sufficient quantities to initiate the first stages of regeneration. If this food was absent and its formation prevented regeneration was prohibited.

Such an explanation as this does not lose sight of the importance of the other factors so strongly emphasized by various workers, for all these factors doubtless play an important part in nutrition.

Experimental data in this particular case are not extensive enough to permit drawing conclusions as to which of the above factors or groups of factors acting separately or together, was the determining one. However, since an intimate relation exists between growth and regeneration and since growth is dependent upon nutrition, it would seem as if some phase of nutrition must be an important factor in regeneration, if not the most important factor.

SUMMARY

1. Regeneration took place near the base of the petiole of a detached leaf of a young sporophyte of *Phegopteris polypodioides*, placed upon sand moistened with Knop's solution in moist air.

2. A cellular mass, resembling a prothallium, was formed, from which rhizoids, intermediate structures between leaves and prothallia, and true leaves developed.

3. At first true leaves resembling those of normal young sporophytes were formed; then leaves of a much simpler type developed.

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